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A quantitative approach to assessing allowable harm in species at risk: application to the Laurentian black redhorse (*Moxostoma duquesnei*)

Approche quantitative pour l'évaluation des dommages admissibles causés aux espèces en péril : application au chevalier noir (*Moxostoma duquesnei*)

Luis A. Vélez-Espino and Marten A. Koops

Fisheries and Oceans Canada/Pêches et Océans Canada
Great Lakes Laboratory for Fisheries and Aquatic Sciences/
Laboratoire des Grands Lacs pour les Pêches et les Sciences Aquatiques
867 Lakeshore Rd./ 867, Chemin Lakeshore
Burlington ON L7R 4A6 Canada

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FOREWORD

This document was not peer-reviewed under the Department of Fisheries and Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process. It presents the allowable harm assessment (AHA) portion of a modelling methodology being developed in support of DFO-SARCEP (Species at Risk Committee / *Comité sur les espèces en péril*) recovery potential assessments (RPA), particularly for data limited species at risk. When the full methodology is developed, it is expected to form the basis for many RPAs and to inform the development of recovery strategies.

AVANT-PROPOS

Le présent document n'a pas été revu selon le processus consultatif scientifique du ministère des Pêches et des Océans, coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif. Le présent document expose le volet « évaluation des dommages admissibles » (EDA) d'une méthodologie de modélisation que l'on est en train d'élaborer pour appuyer les évaluations du potentiel de rétablissement (EPR) du MPO et de SARCEP (Species at Risk Committee / *Comité sur les espèces en péril*), particulièrement lorsque les données sont limitées sur l'espèce en péril étudiée. Une fois mise au point, cette méthodologie devrait servir de fondement pour plusieurs EPR et d'outil pour l'élaboration des programmes de rétablissement.

ABSTRACT

The *Species at Risk Act* (SARA), intended to protect species at risk of extinction or extirpation in Canada and to promote their recovery, determines population resilience to human-induced harm by conducting what has been termed an allowable harm analysis (AHA), but which is now part of the recovery potential assessment (RPA). The function of an AHA is to provide scientific advice about the level of harm a species (or population) can withstand without compromising recovery or survival. Here we develop a methodology to quantitatively estimate allowable harm within a demographic framework. After defining harm as a negative perturbation that can target one or more vital rates and life stages simultaneously, allowable harm is calculated as a function of (a) the vital rate(s) impacted by human action(s), (b) the elasticities of impacted vital rate(s), (c) the population growth rate prevailing before the harm occurs, and (d) the minimum population growth rate that will not jeopardize the survival and future recovery of the population. Additional characteristics of our approach are that it requires minimal data while using all available data, can link population dynamics with habitat supply, is flexible enough to encompass complex life histories, and it follows a precautionary approach. We demonstrate this methodology by applying it to a Canadian population of the threatened black redhorse (*Moxostoma duquesnei*).

RÉSUMÉ

La *Loi sur les espèces en péril* (LEP), dont le but est de protéger les espèces menacées d'extinction au Canada ou susceptibles de disparaître du pays et de favoriser leur rétablissement, nous permet de déterminer la résilience des populations aux dommages causés par l'homme par le biais d'une « évaluation des dommages admissibles » (EDA), un exercice maintenant intégré aux évaluations du potentiel de rétablissement (EPR). Les EDA nous permettent de formuler des avis scientifiques sur le niveau de dommages auxquels une espèce (ou une population) peut être exposée avant que son rétablissement ou sa survie ne soient compromis. La méthodologie dont il est question ici nous permettra d'estimer de façon quantitative les dommages admissibles dans un cadre démographique donné. Après avoir défini les dommages comme étant des perturbations pouvant affecter un ou plusieurs cycles vitaux et stades de développement simultanément, nous calculons les dommages admissibles en fonction : a) d'un ou de plusieurs cycles vitaux touchés par l'activité humaine; b) de l'élasticité des cycles vitaux touchés; c) du taux de croissance de la population qui existait avant l'apparition des dommages; d) du taux minimal de croissance de la population qui ne mettra pas en danger la survie ou le rétablissement de cette dernière. Les autres particularités de notre approche tiennent au fait qu'elle ne requiert qu'un volume minimal de données tout en utilisant toute l'information disponible, qu'elle permet d'établir un lien entre la dynamique de la population et la disponibilité de l'habitat, qu'elle est suffisamment souple pour englober des cycles biologiques complexes et qu'elle repose sur une approche de précaution. Enfin, pour illustrer cette méthodologie, nous l'avons appliquée à une population menacée de chevaliers noirs (*Moxostoma duquesnei*) du Canada.

INTRODUCTION

The *Species at Risk Act* (SARA) is intended to protect species at risk of extinction or extirpation in Canada and to promote their recovery. Under SARA an interim assessment of allowable human-induced harm is needed to permit human activities until a recovery strategy is developed. An allowable harm analysis (AHA) provides an assessment of the level of harm that can be permitted without jeopardizing the survival or recovery of a species. To date, AHA has been applied mainly to commercial marine species for which extensive catch-effort time series are available. Current efforts to assess allowable harm in freshwater species at risk are essentially qualitative, based mostly on expert opinion. Hence, DFO still needs scientific tools to determine allowable harm in freshwater species at risk for which population and life history data are meagre. In addition, habitat loss is an important threat to freshwater species (Dextrase and Madrak 2005) and there is a need to integrate population dynamics and habitat supply research to enable assessment of population responses to anthropogenic activities (e.g., Minns *et al.* 1996).

We present a novel approach to quantitatively assess allowable harm. This methodology is intended to be feasible and applicable to all species at risk (or populations) for which basic life history information can be obtained or inferred. Knowledge about quantitative relationships between habitat supply and demand can further extend the assessments by projecting the effects of habitat alteration on population dynamics. The approach relies on demographic modelling widely applied in conservation biology (e.g., Crouse *et al.* 1987; Cortés 2002; Wilson 2003), resource management (e.g., Getz and Haight 1989; Hayes 2000) and pest control (Rockwell *et al.* 1997; Shea and Kelly 1998; Neubert and Caswell 2000). Within this framework, population growth rate (either deterministic or stochastic) is considered the best indicator of population fitness (Metz *et al.* 1992; Caswell 2001), and allowable harm is understood as a function of two factors: the population growth rate before recovery actions (at the time of species listing) and the species' sensitivity to human-induced harm at different points of its life cycle.

To introduce and apply this methodology, we present a case study using life history and habitat information for black redhorse (*Moxostoma duquesnei*), which is currently designated as threatened in Canada (COSEWIC 2005). Although black redhorse is found throughout much of the Mississippi River and lower Laurentian Great Lakes basin, remnant populations in Canada are confined to small areas in the Grand, Thames, and Maitland river watersheds. In addition, black redhorse was previously chosen as one of seven case studies to identify and quantify critical habitat for species at risk (DFO 2004).

First, we present an interpretation of allowable harm within a demographic and population dynamics framework, followed by a description of the proposed approach to quantitatively assess the sensitivity of population growth rate to human-induced harm in one or more stages of the life cycle, and finish with the integration of habitat-based modelling into the demographic approach to determine the effect of habitat loss on population growth rate. Management recommendations are drawn from two complementary demographic perspectives: projections under a constant environment (deterministic) and projections after the incorporation of uncertainty in life history traits allowing for simulations under a varying environment (stochastic). In addition, transient dynamics and their influence on population size are analyzed in terms of population momentum (Keyfitz 1971). Lastly, conclusions are drawn regarding the management of black redhorse in Canada as well as general conclusions regarding aspects of the application of this methodology to other species at risk.

METHODS

A demographic interpretation of allowable harm

Structured models, such as those applied in conservation biology, may be more valuable than fisheries models for addressing specific management questions (Getz and Haight 1989) such as those related to allowable harm and recovery targets of species at risk. The characteristic paucity of population and life history data for most species facing extinction or extirpation makes data-demanding fisheries models less suitable. The application of demographic techniques have been widely explored and successfully applied to different taxa (e.g., Crouse *et al.* 1987; Brault and Caswell 1993; Hitchcock and Grato-Trevor 1997), including fish (Cortés 2002; Wilson 2003; Vélez-Espino 2005).

The relatively recent advance of matrix population models (see Caswell 2001 for a thorough review) is having important impacts on the management of wild populations, especially since the development of the concept of elasticity (Beissinger and Westphal 1998) and its key role in the prospective exercise called perturbation analysis (Caswell 2000), which evaluates the functional dependence of population growth rate (λ) on the rates of survival, reproduction, and growth (vital rates). Perturbation analysis, as a demographic prospective technique, depends on the construction of projection matrices from which λ can be calculated and the relative importance of each vital rate (i.e., elasticities) can be used to project the effects of management interventions (Caswell 2000). In demographic terms, human-induced harm is a negative perturbation (perturbations can be positive when trying to improve population performance) that can target one or more vital rates and life stages simultaneously. Hence, population growth rate will be susceptible not only to human-induced mortality but also to reductions of reproductive success and growth rates caused by human actions.

Elasticities are demographic derivatives that indicate the functional dependence of the population growth rate on vital rates (de Kroon *et al.* 1986; Caswell 2000). Their computation depends on the analysis of population projection matrices that incorporate age or stage specific vital rates survival, growth and fecundity (see also special feature on elasticity analysis in *Ecology* 81: 605-665). Any life history can be portrayed by a stage-structured matrix including several biologically meaningful stages (see Figure 1 for a stage-structured projection matrix for black redhorse). The elements of a stage-structured matrix generally include the fecundity coefficient of stage class j (F_j), the probability of surviving stage j and remaining in stage j (P_j), and the transition probability of surviving one stage and moving to the next (G_j). A stage-structured model requires defining σ_j as the annual survival probability of an individual in stage j, and γ_j as the probability of moving from j to j+1 given σ_j. Then, the parameters P_j and G_j are defined as $\sigma_j(1-\gamma_j)$ and $\sigma_j\gamma_j$, respectively. Assuming that the age distribution within stages is stable (see Lefkovitch 1965), the term γ_j is calculated by:

1)
$$\gamma_j = \frac{\left(\sigma_j/\lambda\right)^{T_j} - \left(\sigma_j/\lambda\right)^{T_j-1}}{\left(\sigma_j/\lambda\right)^{T_j} - 1}$$

where T_j is the duration (years) of stage j and λ is the largest eigenvalue of the matrix (Caswell 2001). A population will be at equilibrium when $\lambda = 1$, declining when $\lambda < 1$, and growing when $\lambda > 1$. For projection matrices like these, the influence of vital rates on the population growth rate is indicated by the partial derivatives of λ with respect to m_{ij}, the individual elements of the

matrix. Elasticities (ε_{ij}) scale these derivatives to adjust for different magnitudes of the vital rates (e.g., reproductive rates can be several orders of magnitude larger than survival probabilities), and they are calculated as:

2) $$\varepsilon_{ij} = \partial \log \lambda / \partial \log m_{ij} .$$

Elasticities of matrix elements are additive and sum to unity. Multiplying the set of elasticities by λ produces a set of contributions which sum to λ, and the ε_{ij} themselves give the relative contribution of the different transitions to λ (de Kroon *et al.* 1986).

Equation 2 estimates the elasticities of matrix elements, not vital rates (see computation of matrix elements in the following sections), which usually contribute to more than one matrix element. Thus, the chain rule for differentiation is used to compute vital rate elasticities:

3) $$\varepsilon_{v} = v/\lambda \;\; \partial v/\partial \lambda = v/\lambda \;\; \sum \partial \lambda/\partial m_{ij} \;\; \partial m_{ij}/\partial v$$

where *v* is a lower level variable (e.g., vital rate). Lower level elasticities do not in general sum to 1, but they still indicate the relative sensitivity of λ to changes in the life-history traits and vital rates. The vital rate elasticities from equation 3 can be used to compute the effect on λ of human-induced harm upon one or several vital rates:

4) $$\lambda_{new} = \lambda \left(1 - \sum_{v=1}^{n} \varepsilon_{v} \delta_{v} \right)$$

where λ is the population growth rate before allowed harm, *n* is the number of stage classes in the matrix, and λ_{new} is the projected population growth rate after harming one or more vital rates simultaneously. Harm (δ_v) in equation 4 is expressed as the human-induced proportional reduction in *v*.

Thus allowable harm (τ_v, to distinguish from δ_v) is the inverse case (inequality 5), and it will depend on four factors: (a) the vital rate(s) impacted by the involved human action(s), (b) the elasticities of impacted vital rate(s), (c) the population growth rate before allowing the harm (λ_0), and (d) the minimum population growth rate (λ_{min}) that will not jeopardize the survival and future recovery of the population:

5) $$\tau_{v} \leq \left(1/\varepsilon_{v} \right) \left[\left(\lambda_{min} - \lambda_{0} \right) / \lambda_{0} \right]$$

The values of λ_{min} and λ_0 are delineated by the conceptual framework for AHA. Once a species is listed, harm caused by human activities should be restricted to the extent possible as per the conditions set out in SARA section 73(3):

(a) all reasonable alternatives to the activity that would reduce the impact on the species have been considered and the best solution has been adopted;

(b) all feasible measures will be taken to minimize the impact of the activity on the species or its critical habitat or the residences of its individuals; and

(c) the activity will not jeopardize the survival or recovery of the species.

The function of AHA is to provide scientific advice in support of paragraph 73(3)(c) about the levels of harm a species (or population) could sustain without compromising the above conditions.

Among the several criteria used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to determine the status of wild species, criterion "A" guides the status assessment of species based on observed or inferred rates of population decline. Although most freshwater species at risk are listed as endangered or threatened based on criterion "B" (small distribution, habitat fragmentation, and distribution decline), the "designation (status)" rate of decline can be used as a first approximation to a conservative estimate of λ before allowing harm. Without ignoring that under some circumstances populations can exhibit positive growth rates and at the same time experience drastic habitat losses (Vélez-Espino 2005), the use of such an index of population growth can be justified for species at risk for which abundance time series are lacking.

A declining population cannot support further harm without accelerating the process of extinction or extirpation (Caughley and Gunn 1996). However, it is also a tenet of population biology that at low densities, as would be the case for many freshwater species at risk, population growth would be maximized (Reynolds and Freckleton 2005; Sibly *et al.* 2005), particularly if the primary causes of decline are removed (Caughley and Gunn 1996). Nevertheless, a recent meta-analysis by Sibly *et al.* (2005) revealed a concave relationship between population growth rate and density in fishes, indicating that populations would recover from disturbances more slowly than predicted by maximum population growth at low densities. A precautionary approach would be to set initial population growth rate (λ_0) at an intermediate point between these two extremes, designation (λ_d) and maximum (λ_{max}) population growth rates, but also allowing the possibility that the population is regulated by the carrying capacity of the occupied habitat and therefore attracted to equilibrium (Turchin 1995). More specifically, remnant populations of endangered and rare species can still exhibit densities close to the carrying capacity as a result of habitat contraction and fragmentation (Debinski and Holt 2000).

Under COSEWIC's criterion A, a species is listed as endangered if evidence indicates a 70% decline over the last 10 years or three generations (3ζ) (i.e., $\lambda = 0.3^{1/10}$ or $\lambda = 0.3^{1/3\zeta}$), whichever indicates a greater decline, and as threatened if evidence indicates a 50% decline over the last 10 years or three generations (i.e., $\lambda = 0.5^{1/10}$ or $\lambda = 0.5^{1/3\zeta}$), whichever indicates a greater decline. Thus, knowledge of the population's generation time would be sufficient to estimate its designation population growth rate λ_d. It has been demonstrated that maximum population growth (λ_{max}) at low densities is determined by somatic growth and as such by body size. Specifically, Blueweiss *et al.* (1978; also revised in Charnov 1993) showed that there is a strong relationship between the maximum intrinsic rate of increase and adult body weight across a broad range of taxa. Similarly, Randall and Minns (2000) found a predictive equation based on the allometry between production per unit biomass (P/B) and weight at maturity for freshwater fish. In a population dynamic context, maximum P/B is equal to the r_{max} (Peters 1983). Accordingly, P/B as a surrogate of r_{max}, also varies inversely with fish size at maturity and longevity and is therefore appropriate for individual species and populations (Randall and Minns 2000). The corresponding equation is:

6) $$r_{max} = 2.64W^{-0.35}$$

where r_{max} is expressed in year^{-1} and W in grams. Maximum population growth rate λ_{max} is simply $e^{r_{max}}$.

Balancing conservative and optimistic estimates of population growth before allowable perturbations can be accomplished by using the geometric mean population growth rate (Λ) combining designation (λ_d), maximum (λ_{max}), and equilibrium (λ_{eq}) estimates. The assimilation of uncertainty into annual growth rates requires the use of geometric means; population growth rate is a multiplicative process and the geometric mean represents the average population growth rate observed over a long sequence of stochastically varying growth rates (Morris and Doak 2002). The positive influence of r_{max} on the geometric mean will be greater for fishes exhibiting smaller adult size, whereas long-lived fishes with large size at maturity will likely exhibit geometric means with values less than one, in which case no harm should be allowed.

Lastly, selection of λ_{min} is a management decision. However, to be consistent with subsection 73(3)(c) of SARA, the only way to avoid jeopardizing population survival and recovery is to at least maintain the population until a recovery plan is developed. More specifically, a risk-averse assessment of allowable harm should consider $\lambda_{min} = 1$ when using equation 5, though allowing harm with $\lambda_{min} < 1$ may be appropriate in particular situations where (i) recovery plans are envisioned to be implemented in the very near term, (ii) population size is at its upper bound according to COSEWIC (e.g., criterion "C"), (iii) there are no reasonable alternatives for allowed activities, or (iv) extra-regional populations grant survival of the population (i.e., rescue effect). Extra caution should be exercised when the harm is irreversible (e.g., through habitat loss).

Black redhorse life history

Life history data for black redhorse were extracted from the literature (Table 1). This information included age specific survival rates as well as variation in age of first maturity and longevity. In addition, length at age and number of eggs (m) as a function of length were computed from empirical relationships developed for black redhorse by Reid (unpublished data, Fisheries and Oceans Canada) using the von Bertalanffy model and by Kott and Rathmann (1985), respectively. Given that age at maturity is variable among populations (2-5 years; Bowman 1970; Howlett 1999) and that the majority of the population matures at age 4 (Reid and Mandrak 2002), a cumulative binomial distribution was used to estimate the probability of a female maturing at age i, $p(i)$. The parameters for this distribution were extracted from a probability distribution function with probability of maturing per trial of 0.5, and delimited by $p(1) = 0$ and $p(5) = 1$. Lastly, age specific female fertility (f_i) was computed as:

$$7) \qquad f_i = m_i p(i) \varphi_i$$

where φ_i is the proportion of eggs producing females. Based on the observations of Meyer (1962), Bowman (1970), and Parker and Kott (1980) φ_i was given a value of 0.5, representing a balanced sex ratio.

Stage-structured model

Age specific information is only available for a few aquatic species at risk. Despite black redhorse being one of them, the need for a methodology applicable to most species at risk (generally lacking age specific information) prompted our use of a stage-structured model as apart of a parsimonious methodology to estimate allowable harm. Moreover, management plans are more likely to relate to life-cycle stages than to age classes. The black redhorse life cycle was divided into 4 stages: young-of-the-year (YOY; stage 1; from egg to the end of the

first year of life), juveniles (stage 2; from the end of the first year to the age of first maturity), young adults (stage 3; first half of the adult period, which covers the period from first reproduction to maximum observed age at reproduction) and old adults (stage 4; second half of the adult period). Shorter life histories might be represented by only three stages (e.g., YOY, juveniles, and adults), but for long-lived fishes with substantial increments in adult size and associated fertility rates important information may be lost by lumping all adults into a single stage (e.g., Crouse *et al.* 1987).

We used a post-breeding projection matrix (see Caswell 2001), in which fecundity coefficients (F) depend on adult survival through the previous year as well as the stage specific fertility f_j such that:

8) $$F_j = f_j P_j + f_{j+1} G_j$$

where f_j is the average fertility across all age classes within a stage and P_j and G_j are calculated with the average age-specific survival rate within a stage (σ_j). According to equation 8, juveniles moving into the young-adult stage the following year will also contribute to the reproductive output because a post-breeding variant assumes the census is taken after spawning, (Crowder *et al.* 1994). Because f_3 is not representative of the potential reproductive contribution of new female recruits into the young adult stage (reproductive variance for the first reproductive age classes is extremely large), we replaced f_{j+1} in equation 8 by the fertility exhibited at the age of first maturity:

9) $$F_2 = f_\alpha G_2$$

Under these conditions the elasticity of young-adult fertility includes the elasticity of fertility at maturity (f_α).

The computation of P_j and G_j required determination of the original λ-value to estimate γ_j with equation 1. Taking all the age specific information in Table 1 we constructed a Leslie matrix (age-structured) that was used to estimate population growth rate. This matrix indicated a population growth rate of $\lambda = 0.992$, in agreement with equilibrium assumptions made by Mandrak and Casselman (unpublished data) to obtain a preliminary estimate of YOY survival (i.e., 0.0006). Therefore, we rounded to unity the matrix-generated λ-value, representing a population at equilibrium. The resulting preliminary stage-structured matrix for black redhorse was:

$$\begin{bmatrix} 0 & 84 & 1961 & 483 \\ 0.0006 & 0 & 0 & 0 \\ 0 & 0.675 & 0.567 & 0 \\ 0 & 0 & 0.034 & 0.057 \end{bmatrix}$$

The next step in the methodology for AHA is to compute both designation and maximum population growth rates to obtain the geometric mean population growth rates (Λ). Black redhorse life-table analysis produces a generation time (g) of 4.5 years, making $3g$ longer than 10 years and therefore producing a designation population growth rate of $\lambda_d = 0.93$. Three estimates of maximum population growth rate were obtained from weight at maturity using low, best, and high values of age at maturity of 2, 4, and 5 years, respectively, for each of the two predictive equations. Equation 7 produced population growth rates (λ_{max}) of 1.34, 1.38,

and 1.57 for α equal to 5, 4, and 2 years, respectively. The corresponding geometric mean values were Λ = 1.08, 1.09, 1.14.

Before computing elasticities and allowable harm (τ_v), one additional step is required: the adjustment of YOY survival to produce a projection matrix with a population growth of Λ since the preliminary projection matrix used a state value for YOY survival. YOY survival was recalculated by solving for σ_1 without altering any other matrix parameter. This involved an iterative process using elasticities for a first iteration through direct perturbation of projection matrices (see Vélez-Espino *et al.* 2006). The new estimates of σ_1 were 0.00043, 0.00045, and 0.00054.

Allowable harm

Establishing λ_{min} = 1 and Λ as the population growth rate before allowed harm, inequality 5 takes the form

10) $$\tau_v \leq (1/\varepsilon_v)[(1 - \Lambda)/\Lambda]$$

and allowable harm for multiple perturbations can be expressed as

11) $$\sum_{v=1}^{n} \varepsilon_v \delta_v \leq 1 - 1/\Lambda$$

where δ_v is the proportional reduction in vital rate *v* and *n* is the number of vital rates affected. Notice that equations 10 and 11 generate negative allowable harm values, where values closer to zero indicate less population resilience against harm in particular vital rates.

Although allowable harm for both single and multiple perturbations was computed using analytical solutions involving elasticities, we recommend that the effects of large human-induced reductions in vital rates be assessed by directly perturbation of the projection matrices. This relaxes the requirement for small changes in the application of inequalities 10 and 11 when non-linearities are exhibited between vital rates and population growth (see Mills *et al.* 1999, de Kroon *et al.* 2000). The need to do this is reduced given evidence that elasticities provide robust projections for perturbations up to 30% and occasionally up to 50% (Caswell 2001). Notwithstanding the robustness of analytical solutions, we also computed allowable harm from direct perturbations of mean matrices. Direct perturbations iteratively alter the vital rate in question while holding all other matrix elements unchanged until the largest eigenvalue of the matrix equals 1. The first iteration uses the results of the analytical solution.

Population momentum

Using a demographic modelling approach to evaluating changes in population growth rates from human actions, including management, implicitly assumes that structural changes in the population will eventually reach a stable stage distribution. However, unstable population structure can have strong inertial effects on future population size, producing a time lag between when a vital rate is changed and when the actual effect on population size occurs. Therefore, final population size will differ from its projected size after an instantaneous change in a vital rate. This difference is known as population momentum (Keyfitz 1971), which is usually applied to demographic simulations bringing population growth to equilibrium (λ_{min} in the present context). Given that the stable population structure of fishes is heavily skewed towards young stages and their reproductive value is heavily skewed towards adult stages, the relationship between population momentum and life history traits (particularly generation time)

is more complex than in other vertebrate taxa (Koons *et al.* 2006), requiring individual assessments of the effect of management actions upon population size. Thus, inertial population growth prior to equilibrium is of interest for fish species at risk in which equilibrium population size should ideally be above the minimum viable population size (see Gilpin and Soulé 1986). Consequently, population momentum should be particularly important to guiding future recovery plans.

We calculated population momentum (M) according to Keyfitz's (1971) formulation for discrete-time models and instantaneous changes in the vital rates:

12) $$M = \frac{e^T (v_1 w_0) w_1}{e^T w_0}$$

where e^T is a transposed vector of ones, w_0 is the dominant right eigenvector of the original projection matrix (before harm is allowed), and v_1 and w_1 are the dominant left and right eigenvectors of the new matrix (representing a population at equilibrium) produced by instantaneous changes in the vital rates (after harm). The right eigenvector w represents the stable stage distribution, which indicates the proportion of the population in stage *j* once enough time has passed that fluctuations due to initial conditions have finished, and the left eigenvector describes the reproductive value of an individual in stage *j* (de Kroon *et al.* 1986). Measures of M are centered on 1. If M > 1 the population will grow to a larger ultimate size following a perturbation and before reaching λ_{min}, and M < 1 indicate that the population will decline to a smaller ultimate size (Koons *et al.* 2006).

The tendency to reach the stable distribution is the main attractor of deterministic projections and should be used as a rough guide of population demographics for perturbations expected to produce stationary growth. Given that the accuracy of projected increments in population size will strongly depend on the geometric mean population growth used in the computations of allowable harm, the projected direction of population change will be more useful than its magnitude. Thus, additional information on the dynamics of a population generated from estimates of population momentum is used in our methodology to adjust maximum allowable harm when M < 1 by reducing $\tau_{v,\,max}$ until population momentum is at least 1. The most direct way of adjusting $\tau_{v,\,max}$ is through direct perturbation of the transition matrix, regressing M on $\tau_{v,max}$ and computing $\tau_{v,\,max}$ for M = 1.

Habitat-based modelling aspects

Much of the work conducted on freshwater fish species at risk involves habitat supply studies and there is an awareness of the need to merge population dynamics and habitat research (Minns *et al.* 1996). This merger seems particularly important for AHA given that the conservation status of most freshwater fishes relies on habitat criteria. Habitat supply models by Minns *et al.* (1996) and Minns (2003) are based on the assumption that stage-specific survival decreases in proportion to the ratio between habitat supply (A_j) and habitat requirements (a_j) below a threshold identified as the critical habitat area (CA_j):

13) $$\sigma_i \propto A_i / a_i \quad for \quad A_i \leq CA_i$$

where a_j is the product of fish density (N_j) and the area per individual in stage *j* (API_j). If area of suitable habitat is above CA_j survival will be independent of A_j, but if the amount of suitable habitat is below CA_j survival will increase with A_j and decrease with API_j for a given density.

Therefore, at saturation, habitat supply and habitat requirements are balanced and the critical density at which survival is independent of habitat supply is:

14) $$N_i = \frac{A_i}{API_i}$$

Given that API_j is determined by a species life history (Minns *et al.* 1996, Minns 2003), reducing the availability of suitable habitat (A_j) reduces survival rates.

Predictive equations of API_j based on body size have been developed for some freshwater species at risk, including black redhorse. Based on this predictive equation (Table 1) and estimates of the available suitable habitat per stage, Mandrak and Casselman (unpublished data) determined that YOY was the black redhorse life stage most susceptible to habitat loss. Building upon the work of Minns *et al.* (1996) we developed the concept of habitat-loss equivalents (h_j), which measure the relative impact on survival rates caused by habitat reductions in stage *j*. Habitat-loss equivalents standardize the stage-specific ratio between habitat supply and habitat demand by producing relative values. Essentially, habitat-loss equivalents convert absolute ratios into rates that can be effectively incorporated into a matrix model:

14) $$h_j = \frac{A_j}{API_j \sum_{j=1}^{z} A_j / API_j}$$

where *z* is the number of life stages, including spawners as a sub-stage of the entire adult population. Habitat-loss equivalents add to unity and the net effect of proportional habitat reductions on survival rates is computed as $\sigma_j(1- h_j)$. Incorporating h_j as a rate in the matrix allows direct assessment of the sensitivity of population growth rate to proportional area reductions in suitable habitat. Spawning habitat is included as a separate habitat unit due to the effect that altering spawning habitat can have on egg-to-hatch survival through density-dependent mortality and low survival at suboptimal spawning sites (Vélez-Espino *et al.* submitted). Consequently, and for the purpose of this analysis, changes in the spawning area indirectly affecting YOY survival were accounted for by adding the spawning habitat-loss equivalent to that of YOY. However, additional effects on fertility rates do result from reductions in spawning habitat, in which case any reduction of spawning habitat will have a directly proportional effect on fertility rates (see Vélez-Espino *et al.* submitted). Area per individual per stage (API_j) was computed as the geometric mean of area per individual (m^2) at the points in the life cycle delimiting each stage: emergent fry (API = 0.001) and age 1 for API_{YOY}, age 1 and age of first maturity (age 2) for $API_{Juvenile}$, age of first maturity and age 7 for $API_{Young\ adult}$, and age 7 and maximum reproductive age (age 11) for $API_{Old\ adult}$. Spawning area per individual ($API_{Spawner}$) was considered independent of size and its value was based on observations made by Bowman (1970). Using estimates of habitat supply per life stage for the black redhorse population occupying the Grand River between the Paris and Wilkes dams, Brantford (Mandrak and Casselman unpublished data), we computed habitat-loss equivalents for each stage after dividing the habitat supply estimated for age-one and older fish equally among our model stages for juveniles, young adults, and old adults.

Incorporating habitat-based parameters into the projection matrix

The effects of habitat loss upon vital rates can now be translated into effects on population growth rates to determine the maximum allowable harm associated with human activities involving habitat. Converting habitat loss into a rate that can be incorporated in the population matrix allows direct estimates of the sensitivity of population growth rate to stage-specific habitat loss. This is an important step in the methodology because effects of habitat loss are likely to differ dramatically in magnitude for different stages. The relative effect on survival rates of decreasing habitat area was included as a rate in the projection matrix of black redhorse separating the effects on survival rates from the effects on fertility rates. Given that reductions in spawning habitat are proportional to reductions in fertility rates, the projection matrix explicitly incorporates habitat effects on survival (σ_j), which is a multiplicative lower-level parameter in matrix elements G_j, P_j, and F_j:

$$\begin{bmatrix} 0 & F_2(1 - h_{Juvenile}) & F_3(1 - h_{Young\ adult}) & F_4(1 - h_{Old\ adult}) \\ G_1(1 - (h_{YOY} + h_{Spawner})) & 0 & 0 & 0 \\ 0 & G_2(1 - h_{Juvenile}) & P_3(1 - h_{Young\ adult}) & 0 \\ 0 & 0 & G_3(1 - h_{Young\ adult}) & P_4(1 - h_{Old\ adult}) \end{bmatrix}$$

Incorporating uncertainty in the vital rates and habitat-based parameters

Uncertainty about the values of life-history traits underpinning vital rates and habitat-based parameters must be included in the determination of allowable harm. This requires generating variation bounds to vital rates and habitat-loss equivalents based on the biological limits of life-history traits.

Variation in age at maturity (α) and longevity (t_{max}) can cause important changes in the stage-structure of a population, which is defined by the assigned stage duration (T_j). Any change in T_j will affect the vital rates of juvenile, young-adult, and old-adult stages as well as the area per individual (API_j) underpinning the habitat-loss equivalents (h_j). YOY survival is not affected by these changes because the stage duration is fixed, though uncertainty in this vital rate has already been introduced into the model. Based on available knowledge about the life history of black redhorse we compute new values of σ_j, γ_j, f_j, and h_j caused by changes in stage duration resulting from all possible combinations of biologically likely values of age at first maturity (2-5 years) and longevity (8-11 years). Values generated from a life cycle with an average age-at-maturity of 4 years and an average longevity of 9 years were considered as best or most likely whereas lowest and highest values among all the combinations were selected to define the limits of vital rates and habitat-loss equivalents used in the simulation modelling (see Table 2).

We generated 1000 random matrices where vital rate values were drawn from uniform distributions defined by the limits for each vital rate in Table 2. Population growth rate (λ) was calculated for each matrix, elasticities of survival and fecundity rates were calculated for each matrix, and a parametric bootstrap was used to estimate 95% confidence intervals for each elasticity value. This procedure was repeated after including uncertainty in habitat-loss equivalents to generate stochastic mean and 95% confidence intervals for the elasticities of h_j. All computations of population growth rates, population momentum, elasticities, and simulations were conducted with the aid of MATLAB version 7 (The Mathworks, Inc., Natick, Massachusetts).

RESULTS

Elasticities

Deterministically, the proportional sensitivity (i.e., elasticity) of black redhorse population growth rate to changes in the vital rates indicated that (a) perturbations in survival rates have a greater effect on the dynamics of the population than perturbations in fertility rates, (b) perturbations of the vital rates of old adults (age-7 and older) have a relatively small effect on the population - particularly perturbations in old adult survival have a negligible effect, and (c) perturbing young adult survival causes the greatest effect on population growth rate (Figure 2a). Incorporating uncertainty in the vital rates qualitatively changed the conclusions drawn from the deterministic approach by increasing the relative importance of juvenile survival and diminishing the relative importance of young adult survival. The mean values of the remaining vital rates did not change substantially compared to those computed from mean matrices (Figure 2b). Wide confidence intervals prevent strong conclusions based on quantitative differences among elasticities, except old adult rates for which elasticity values remained low with small confidence intervals. Thus, deterministic conclusions regarding the elasticities of old adult vital rates remained robust, indicating that black redhorse population growth rate is expected to be highly resilient to harm exerted upon age-7 and older fish. However, the stochastic approach suggests that black redhorse population growth rate is similarly and moderately sensitive to perturbations of YOY, juvenile, and adult survival, and young adult fertility.

Allowable harm

As a result of the deterministic elasticity pattern, harm in the form of reductions in young adult survival, $\tau_{\sigma(\text{Young adult}),\, max}$, is expected to have the largest impact on black redhorse population growth rate (Table 3). Taking a risk-averse position, consistent with subsection 73(3) of SARA, we discuss results corresponding to the lowest population growth geometric mean ($\Lambda = 1.08$). An allowable harm greater than a 30% reduction in σ_{YOY} or $\sigma_{Juvenile}$, a 14% reduction in $\sigma_{\text{Young adult}}$, or a 36% reduction in $f_{\text{Young adult}}$ is expected to jeopardize the survival and future recovery of the population. Note in Table 3 that maximum allowable harm for old adult vital rates exceeds the maximum biologically possible value (i.e., -1), indicating that a 100% reduction of either $\sigma_{\text{Old adult}}$ or $f_{\text{Old adult}}$ (or for that matter the elimination of the old adult stage) does not bring down population growth rate to the minimum acceptable (i.e., equilibrium), and therefore black redhorse population dynamics are expected to be highly resilient to harm upon old adult vital rates.

Direct perturbation of the three baseline matrices with YOY survival values of 0.00054, 0.00045, and 0.00043 showed that simulating smaller values of maximum allowable harm ($\tau_{v,\, max}$) and smaller changes in population growth rate ($\lambda_{min} - \Lambda$) produced more accurate results, closer to $\lambda_{min} = 1$ (Table 3). In general, the effect of perturbations up to 30% was well represented by elasticities. However, projections with elasticities overestimated maximum allowable harm. A clear example of this is that the maximum allowable harm computed for young adult fertility caused a population decline of 3% annually instead of equilibrium when using $\Lambda = 1.14$. Therefore, $\tau_{v,\, max}$ should be even smaller than the risk-averse values computed from elasticities. In the case of black redhorse, inequalities 10 and 11 proved reliable for harm of up to 30%; greater harm should use these inequalities as approximations, refining their values through direct perturbations. The application of this approach produced values of maximum allowable harm of $\tau_{\sigma(YOY),\, max} = \tau_{\sigma(\text{Juvenile})\, max} = -0.25$, $\tau_{\sigma(\text{Young adult}),\, max} = -0.13$, and $\tau_{f\,(\text{Young adult}),\, max} = -0.32$. These values suggest slightly lower allowable harm for all vital rates and confirmed previous conclusions regarding the relative importance of each vital rate.

Translating the stochastic pattern of elasticities into maximum allowable harm demonstrated that in spite of important uncertainty in elasticity values, the margin of variation for maximum allowable harm was not particularly large for vital rates of YOY, juvenile, and young adult stages, except young adult fertility that exhibited a wide confidence interval (Table 4). These results indicate that a low to moderate maximum harm can be allowed in these vital rates without impairing the capacity of the black redhorse population to survive and eventually recover. From a risk-averse perspective, using the lower bound of the 95% confidence intervals as a reference for the determination of maximum allowable harm, maximum allowable reductions of 19% for YOY survival, 14% for juvenile survival, or 17% for young adult survival and young adult fertility are expected to protect the population against declines. Remember though that these numbers represent individual effects. Any human activity simultaneously impacting more than one of these rates can collapse a population if the sum of effects produces a population decline (i.e., $\lambda_{new} < 1$).

The analysis of population momentum indicates that modelled black redhorse population size is expected to increase about four times its current size under maximum allowable harm conditions targeting a single significant vital rate. Therefore, estimates of maximum allowable harm are kept unaltered. Population momentum, calculated only for deterministic risk-averse values of maximum allowable harm to significant vital rates σ_{YOY}, $\sigma_{Juvenile}$, $\sigma_{Young\ adult}$, and $f_{Young\ adult}$, resulted in a population growing 4.5, 4.2, 3.6, and 3.6 times its original size, respectively, before stabilizing. These population momentum values might be combined with estimated or inferred population size to determine whether black redhorse equilibrium population size also represents a viable size given its life history and habitat constraints.

Habitat

The presence of more stages in our model did not changed the original conclusion of Mandrak and Casselman (unpublished data) concerning YOY being the stage with a survival rate most sensitive to habitat loss (Table 5). Our results from the deterministic approach indicated that a 50% habitat reduction (for example) in individual stages is expected to cause a 31% reduction in σ_{YOY}, a 17% reduction in $\sigma_{Juvenile}$, a 2% reduction in $\sigma_{Young\ adult}$, and a 0.5% reduction in $\sigma_{Old\ adult}$. Elasticity analysis of the habitat-based matrix indicated that the sensitivity of population growth rate to habitat loss is greater for YOY, followed by juveniles, for which the effect is one third that of YOY. Reducing young adult habitat has a low effect on population growth rate, whereas reducing old adult habitat has a negligible effect (Table 5). Notice that this kind of conclusions pertain only to the case where habitat is well separated among stages and therefore the stage-specific effects of habitat loss are independent. The separation of adult stages into young and old had demographic bases but does not correspond to habitat use; young adult and old adult black redhorse seem to share the same habitat, which appears to overlap strongly with the habitat of juveniles. Therefore, it would be more convenient and less misleading to add the elasticities of the habitat-loss equivalents, $\varepsilon(h)$, of these three stages (juvenile, young adult, and old adult) to conclude that the sensitivity of black redhorse population growth to loss of habitat shared by age-one and older individuals (excepting spawning habitat) is represented by an elasticity of -0.115. This indicates that a 10% area reduction (e.g., in this habitat) would translate into a 1.15% reduction in the population growth rate. Similarly, a 10% reduction in YOY habitat would represent a 3% reduction in population growth rate. Summarizing, maximum allowable harm in the form of removing habitat shared by age-one and older fish (except spawning habitat) was then estimated as $\tau_{h(\text{age-one and older}),\ max} = -0.64$, and for YOY $\tau_{h(YOY),\ max} = -0.25$. These numbers indicate that reducing the habitat of age-one and older individuals (except spawning habitat) by more than 64% or the habitat of YOY

by more than 25% is expected to jeopardize the survival and recovery of black redhorse populations. Similar results were obtained with direct perturbations.

In spite of the meagre effects that the removal of spawning habitat has on black redhorse YOY survival, we still expect effects on fertility rates that are independent of survival rates and proportional to habitat reduction (Vélez-Espino *et al.* submitted). The relative importance of fertility rates (i.e., their elasticities) will be the main parameters determining the sensitivity of population growth rate to reductions of spawning habitat (*SH*), and maximum allowable harm in the form of reductions of spawning habitat will be:

$$16) \qquad \tau_{SH,\max} = \left[\varepsilon\left(f_{\text{Young adult}}\right) + \varepsilon\left(f_{\text{Old adult}}\right) + \varepsilon\left(f_{\text{Spawner}}\right)\right]^{-1}\left[1 - \Lambda/\Lambda\right]$$

Using the risk-averse value for Λ, we obtained $\tau_{SH,\,max}$ = -0.29, indicating that any reduction of spawning habitat larger than 29% would jeopardize population survival and future recovery.

Thus, if an allowed human activity exclusively involves habitat removal, $\varepsilon(h)$ can be used to project effects on population growth rates from impacts on stage-specific survival rates. However, when habitat removal includes spawning habitat, effects are expected on both YOY survival and fertility rates, in which case the process is more involved as indicated by equation 16. Effects unrelated to habitat removal can be computed from $\varepsilon(\sigma)$ and $\varepsilon(f)$ or through direct perturbation of matrix elements as demonstrated earlier.

The rank of habitat-loss equivalents (h_j) elasticities depicted by the deterministic approach was conserved in the stochastic model (Figure 3), but the magnitude of the elasticity of h_{YOY} increased substantially. In addition, the large confidence interval for this parameter indicated that sensitivity of population growth rate to YOY habitat loss can be moderate to extremely high, particularly when simulations incorporate uncertainty in both vital rates and habitat-loss equivalents (Figure 3a). However, the simulation of uncertainty exclusively in habitat-loss equivalents (Figure 3b) indicates that a large part of the observed elasticity variance (Figure 3a) is attributed to the variation in associated survival rates. This is particularly obvious for the elasticity of YOY survival where there is both a substantial reduction in the width of the confidence interval and a reduction in the mean elasticity value from -0.58 to -0.44 when only variation in habitat-loss equivalents is simulated.

Applying the same risk-averse principle to maximum allowable harm of habitat-loss equivalents obtained with the stochastic approach, habitat loss should be less than 12% in YOY habitat, less than 37% in age-one and older fish habitat (except spawning habitat), and less than 13% in spawning habitat (Table 6). Similarly, the lower bound of the stochastic approach indicates that maximum allowable habitat loss for spawning habitat should be less than 13%. These levels of allowable habitat loss are smaller than those obtained deterministically in spite of the mean values being highly preserved.

Summary table

To increase the likelihood of making decisions consistent with the conservation concerns expressed in SARA, following a precautionary approach, we summarized maximum allowable harm values for vital rates and habitat loss generated by deterministic and stochastic approaches in a comprehensive table (Table 7). In this table, deterministic results from analytical solutions (elasticities) and direct perturbations of projection matrices are contrasted with mean and lower bounds of the confidence intervals from the stochastic approach. Given the levels of uncertainty produced by the stochastic approach, we recommend using the lowest value of maximum allowable harm among those generated by these two approaches.

DISCUSSION

Black redhorse

After application of the precautionary approach (see Table 7), allowable harm for survival rates of YOY, juveniles, and young adults should be less than 19%, 14%, and 13%, respectively. Similarly, reductions of fertility rates of young adults should be less than 17%. Further, black redhorse population dynamics are expected to be highly resilient to extreme reductions in survival and fertility rates of age-7 and older individuals. Reductions in habitat used by YOY, age-one and older (except spawning habitat), and spawners should be less than 12%, 37%, and 13%, respectively, for the black redhorse population occupying the segment of the Grand River between the Paris and Wilkes dams, Brantford. Transferability of allowable harm through habitat loss to other black redhorse populations will depend on the allocation of available habitat among the life cycle stages. Chiefly, it is expected that reductions in YOY habitat will have the largest impact on population growth rate relative to reductions in habitat area of age-one and older or spawners.

Additional sources of uncertainty

Our stochastic modelling allowed for random independent variation in vital rates. Nevertheless, temporal correlation and covariance can strongly influence the values of elasticities (Saether and Bakke 2000). In general, variation in demographic rates is not independent and is likely to be correlated. This correlation can have important impacts on population growth rate (Caswell 2001) and is likely to alter the width of confidence intervals (see Doak *et al.* 1994). Determining correlations between demographic rates in wild populations requires a long time series of life history traits and abundance. This kind of information is scarce for many commercial aquatic species and for the large majority of aquatic species at risk it is practically non-existent. Thus, it is difficult to anticipate additional and critical effects of covariance between life history traits on the allowable harm analysis for black redhorse or any other species at risk.

Another source of uncertainty originates from the assumption of habitat saturation implicit in the computation of habitat-loss equivalents. There is theoretical support indicating that fish populations exhibit a tendency to spend most of their time at or above the carrying capacity (Sibly *et al.* 2005). However, if evidence indicates that assuming saturation is strongly misleading, then a saturation coefficient (C_s) can be introduced as a multiplier of habitat-loss equivalents, in which case the sum of the products for all stages will sum to C_s:

22) $$C_s = \left(A_j / API_j N_j\right)^{-1} = \sum_{j=1}^{n} C_s h_j$$

Obviously, substantial departure from saturation is expected to affect the elasticities of habitat-loss equivalents, causing changes in estimates of maximum allowable harm in the form of habitat loss. We expect that strong departures from saturation will have greater impacts on estimates of allowable harm to black redhorse YOY habitat than any other life stage. Notice that these considerations pertain exclusively to habitat-loss equivalents and do not influence vital rate elasticities or their corresponding allowable harm estimates.

Lastly, this methodology relies on the assumption that after a species is listed, protection is granted, and the main causes of decline are removed. This is reasonable when anthropogenic activities constitute the main population stressors. However, in some cases

natural and complex factors operating on temporal and spatial scales different from those of human activities can play an important role in the impairment of population dynamics. Therefore, violations of the assumption that causes of decline have been removed will influence population growth rates, reducing the room for allowable harm in any form. In addition, demographic, genetic, and environmental factors can interplay and produce extinction vortices in small populations even after the cessation of the most obvious and deterministic causes of decline (Gilpin and Soulé 1986). The best-case scenario would be that major causes of decline have ceased and the population growth rate is maximized, in which case AHA would be suitable. The worst-case scenario would be that listing and protection do not remove population stressors and population growth remains negative. In this case, AHA would not be suitable and recovery strategies would have to be implemented in the short term.

Accordingly, the safest guide against all the aforementioned and other sources of uncertainty is to take a risk-averse position and restrict activities to those with the very lowest impacts on population dynamics. A pragmatic approach is to consider that our model captures the important dynamics of the system and provides the relative impact of allowable harm to help guide management decisions, rather than producing precise estimates of demographic parameters.

About the methodology

Given the often limited data available about the life history and population dynamics of species at risk, an important advantage of this methodology is that its application does not depend on the availability of long time series but it can benefit from this kind of information. Data requirements are reduced to the availability of information on age at maturity, longevity, fertility, survival rates, and predictive equations for length-at-age weight-at age or length-weight regressions. The stochastic approach needs additional information regarding variation in life history traits. In addition, this methodology can be implemented for species for which age- or stage-specific data requirements are not met. Particularly, matrix population models that can be parameterized with partial demographic data (partial life-cycle models) have been developed as an alternative to age-structured or complete stage-structured models (Heppell *et al.* 2000; Oli and Zinner 2001). The paucity of information about survival rates can also been addressed with the use of life history invariants (Charnov 1993), allowing mortality estimates from information on traits such as age at maturity, somatic growth, or longevity (e.g., Cortés 1998; Vélez-Espino *et al.* 2006), though care should be taken in the use of life history invariants (Koops and Chu 2007).

When more than one output was generated, our approach was to use parameter values reflecting a risk-averse position. Accordingly, we used the lowest geometric mean population growth rate (Λ), the lower bound of the confidence intervals for maximum allowable harm (τ_{max}), and the lowest value of maximum allowable harm among the levels predicted by both deterministic and stochastic approaches. This risk-averse position is consistent with the precautionary approach embodied in several international agreements, including the UN Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement and the FAO Code of Conduct (Richards and Maguire 1998). Moreover, our methodology explicitly precludes any harm for situations where the lowest geometric mean population growth rate indicates a declining population scenario ($\Lambda < 1$), in which case no further harm should be allowed.

One important aspect of this methodology is that the demographic modelling is independent of the habitat-based component of the model. If information on habitat supply and demand is not available, maximum allowable harm on vital rates can still be estimated. The effect of habitat loss on population growth rates, as implemented, represents only the impact of changes in habitat quantity on population dynamics through effects on survival. However,

limitations in habitat quantity can also affect growth (e.g., Van Winkle *et al.* 1993) or increase the propensity to emigrate (e.g., Grant and Kramer 1990). The impact of changes in habitat quality, which can be as important as habitat quantity, can be readily incorporated into the model once relationships between some habitat component (biotic or abiotic) and affected vital rate(s) have been empirically determined (e.g., Hayes *et al.* 1996; Eby *et al.* 2005).

Another important aspect of our modelling is that it can guide management efforts through the identification of vital rates with larger contributions to population growth rates. Ideally, recovery targets would benefit from projections of population size resulting from increments in vital rates given natural limits and habitat constraints. Population momentum and elasticities can play an important role in the definition of recovery targets, particularly when the impact of allowable harm on population dynamics shrinks population size and when equilibrium population size is projected to be too small to cope with environmental and/or demographic stochasticity (Gilpin and Soulé 1986; Lande 1993). Interestingly, transient population declines can take place in both growing populations after perturbations decrease vital rate values to produce equilibrium or in declining populations after perturbations increase vital rates to produce equilibrium (Caswell 2001; Koons *et al.* 2006).

Finally, the next step in the development of a general quantitative recovery potential assessment (RPA) will be the implementation of this methodology to significantly different life histories to detect additional modelling requirements and to contrast management recommendations in light of life history and population dynamics theory. The feasibility of projecting population responses (Shelton *et al.* 2007) in species with differing sensitivities to anthropogenic perturbations should improve management of species at risk.

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Table 1. Trait values and predictive equations used for AHA of black redhorse.

Trait / relationship	Symbol	Value / Equation	Source
Age 0 Survival	P0	0.00058	Mandrak anc Casselman (unpublished data)
Age 1 Survival	P1	0.675	Root *et al.* 1997
Age 2 Survival	P2	0.5	Root *et al.* 1997
Age 3 Survival	P3	0.813	Root *et al.* 1997
Age 4 Survival	P4	0.622	Root *et al.* 1997
Age 5 Survival	P5	0.585	Bowman 1970
Age 6 Survival	P6	0.485	Bowman 1970
Age 7 Survival	P7	0.18	Bowman 1970
Age 8 Survival	P8	0.025	Bowman 1970
Age 9 Survival	P9	0.015	Bowman 1970
Age 10 Survival	P10	0.01	Bowman 1970
Age 11 survival	P11	0	Bowman 1970
Age at maturity	α	2 - 5	Bowman 1970, Howlett 1999
Longevity	t_{max}	8 - 11	Schumate 1988, Bowman 1970, Hawlett 1999
Number of eggs	*m*	4126 - 11551	Kott and Rathmann 1985
Proportion of females	φ	0.50	Meyer 1962, Bowman 1970, Parker and Kott 1980
von Bertalanffy equation for Grand River	L-*t*	$L_t = 490.9\,(1 - e^{-0.26\,(t\,+\,0.75)})$	Reid (unpublished data)
Fertility-length equation	*m*-L	$m = (2.46*10^{-6})\,L^{3.713}$	Kott and Rathmann 1985
Weight-length equation	W-L	$W = 8.543*10^{-6}\,L^{3.0256}$	Clark and Reid (unpublished data)
Area per individual	API	$API = e^{-13.28}\,L^{2.904}$	Randall *et al.* 1995

Table 2. Low, best, and high values of survival (σ), transition probability (γ),fertility (*f*), and habitat-loss equivalents (*h*) used for simulation modelling and computation of elasticity confidence intervals.

		Trait			
Stage	**Value**	**σ**	**γ**	***f***	***h***
YOY	low	0.00043	1	-	0.591
	best	0.00045	1	-	0.748
	high	0.00054	1	-	0.778
Juvenile	low	0.588	0.118	-	0.166
	best	0.663	0.209	-	0.193
	high	0.675	1	-	0.335
Young adult	low	0.417	0.056	2955	0.017
	best	0.564	0.169	4537	0.021
	high	0.673	0.349	5919	0.044
Old adult	low	0.017	0.0002	6528	0.009
	best	0.103	0.093	7579	0.012
	high	0.417	1	8831	0.014
Spawners	low	-	-	-	0.021
	best	-	-	-	0.026
	high	-	-	-	0.027

Table 3. Deterministic maximum allowable harm ($\tau_{v,\,max}$) expressed as proportional reductions of the survival (σ) and fertility (f). In parentheses is the new population growth rate after direct perturbations upon the three baseline projection matrices with Λ values of 1.14, 1.09, and 1.08, respectively. For any τ_v less than -1.0, population growth rate cannot be brought to equilibrium even after a 100% reduction in v.

	Vital rates					
Λ	σ_{YOY}	$\sigma_{Juvenile}$	$\sigma_{Young\ adult}$	$\sigma_{Old\ adult}$ *	$f_{Young\ adult}$	$f_{Old\ adult}$ *
1.14	-0.493 (0.968)	-0.493 (0.968)	-0.246 (0.99)	-61.404 (1.138)	-0.581 (0.973)	-3.24 (1.096)
1.09	-0.34 (0.986)	-0.34 (0.986)	-0.161 (0.995)	-39.318 (1.087)	-0.401 (0.989)	-2.232 (1.048)
1.08	-0.306 (0.987)	-0.306 (0.987)	-0.144 (0.993)	-35.273 (1.075)	-0.362 (0.989)	-2.013 (1.036)

(*) Direct perturbation used a 100% reduction in the vital rate.

Table 4. Mean and 95% confidence intervals (95% CI) for stochastic maximum allowable harm in survival (σ) and fertility (*f*). Last column shows integrated fertility rates for all reproductive stages.

	$\tau_{v,\,max}$						
	σ_{YOY}	$\sigma_{Juvenile}$	$\sigma_{Young\ adult}$	$\sigma_{Old\ adult}$	$f_{Young\ adult}$	$f_{Old\ adult}$	f
mean	-0.25	-0.18	-0.25	-10.29	-0.32	-1.24	-0.25
95% CI	(-0.19, -0.38)	(-0.14, -0.25)	(-0.17, -0.39)	(-2.37, -370.37)	(-0.17, -0.92)	(-0.62, -3.94)	(-0.13, -0.74)

Table 5. Area per individual (*API*), habitat supply (*A*), habitat-loss equivalents (*h*), and deterministic elasticities of *h* (ε(*h*)) for each black redhorse life stage. *API* and *A* are given in area units (m^2).

	YOY	**Juveniles**	**Young adults**	**Old adults**	**Spawners**
API	0.03	2.1	19.63	77.22	0.16
A	9000	391050	391050	391050	1875
h	0.6	0.34	0.04	0.01	0.02
ε(*h*)	-0.3	-0.097	-0.018	-0.000	-0.01

Table 6. Mean and 95% confidence intervals (95% CI) for stochastic maximum allowable harm in stage-specific habitat-loss equivalents, including the parameters corresponding to integrated habitat-loss equivalents of age-one and older fish. Last column shows maximum allowable harm over spawning habitat (*SH*).

	$\tau_{h(j),\,max}$					
	h_{YOY}	$h_{Juvenile}$	$h_{Young\ adult}$	$h_{spawner}$	$h_{age\text{-}one\ and\ older}$	** *SH*
mean	-0.17	-0.55	-5.65	-5.01	-0.5	-0.24
95% CI	(-0.12, -0.25)	(-0.41, -0.81)	(-3.82, -10.29)	(-3.67, -6.67)	(-0.37, -0.75)	(-0.13, -0.62)

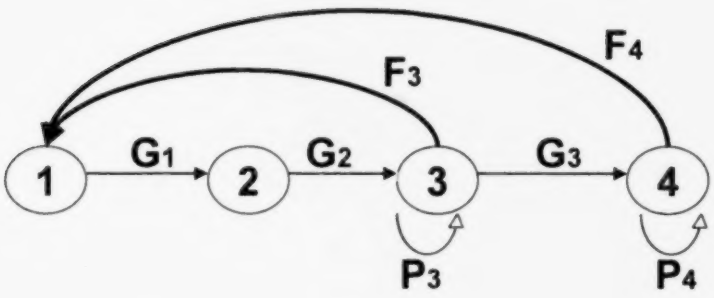
* The Old-adult stage is not included as an independent column because elasticities have magnitudes close to zero, but this stage is included in the composite stage Age-one and older.

** Computed with equation 16, which considers both effects on YOY survival and fertility rates.

Table 7. Summary of maximum allowable harm estimates from deterministic and stochastic approaches for significant vital rates ($\tau_{v,\,max}$) and habitat-based stages ($\tau_{h(j),\,max}$). At the bottom of the table are shown the population momentum values for each vital rate. Bold values indicate the recommended maximum allowable harm for management decisions.

	$\tau_{v,\,max}$ (significant rates)				$\tau_{h(j),\,max}$		$\tau_{SH,\,max}$
Approach	σ_{YOY}	$\sigma_{Juvenile}$	$\sigma_{Young\ adult}$	$f_{Young\ adult}$	h_{YOY}	$h_{age\text{-}one\ and\ older}$	Spawning habitat
Deterministic (elasticities)	-0.31	-0.31	-0.14	-0.36	-0.25	-0.64	-0.29
Deterministic (direct perturbation)	-0.25	-0.25	**-0.13**	-0.32	-0.26	-0.65	-0.26
Stochastic (mean)	-0.25	-0.18	-0.25	-0.32	-0.17	-0.56	-0.24
Stochastic (lower bound)	**-0.19**	**-0.14**	-0.17	**-0.17**	**-0.12**	**-0.37**	**-0.13**
Population momentum	4.5	4.2	3.6	3.6			

(*a*)



(*b*)

$$\begin{pmatrix} 0 & 0 & F_3 & F_4 \\ G_1 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Figure 1. Generalized black redhorse life cycle (*a*) and corresponding stage-structured projection matrix (*b*). The life cycle was divided into four stages: young-of-the-year (stage 1), juvenile (stage 2), young adult (stage 3), and old adult (stage 4). F_i represents stage-specific fecundity coefficient, P_i the probability of surviving and remaining in the same stage, and G_i the probability of surviving and moving to the next stage.

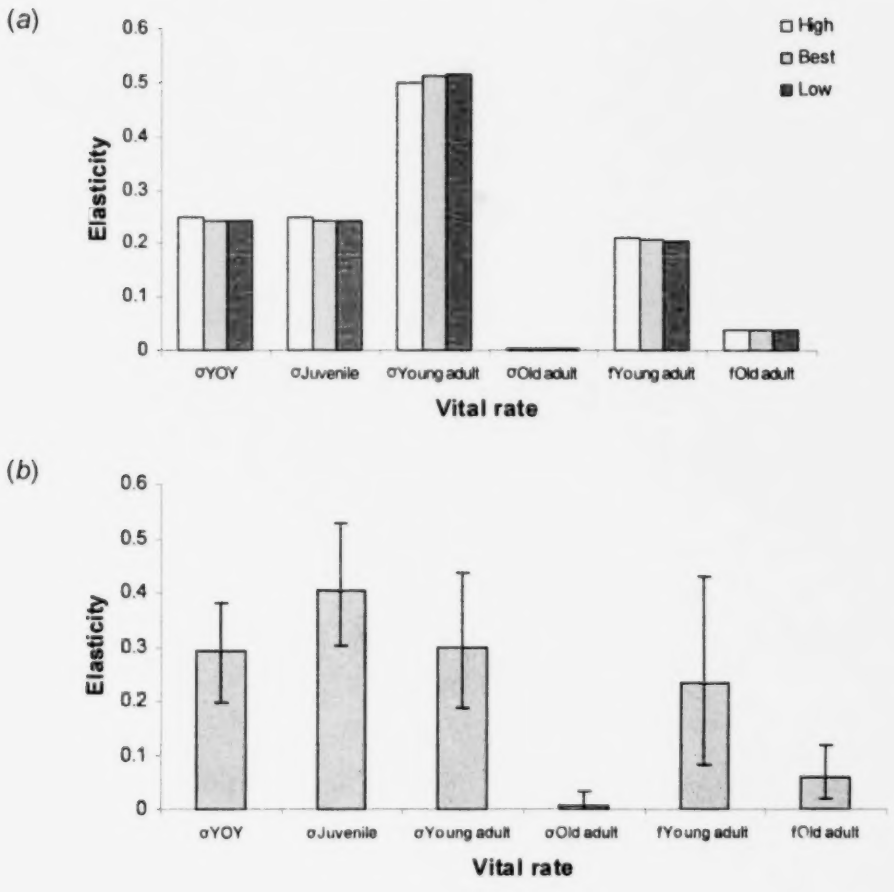


Fig. 2. (a) Vital rate (survival (σ) and fertility (*f*)) elasticities computed from baseline projection matrices with σ_{YOY} values of 0.00054 (high), 0.00045 (best), and 0.00043 (low). (b) Vital rate elasticities computed from parametric bootstrap. Bars indicate 95% confidence intervals.

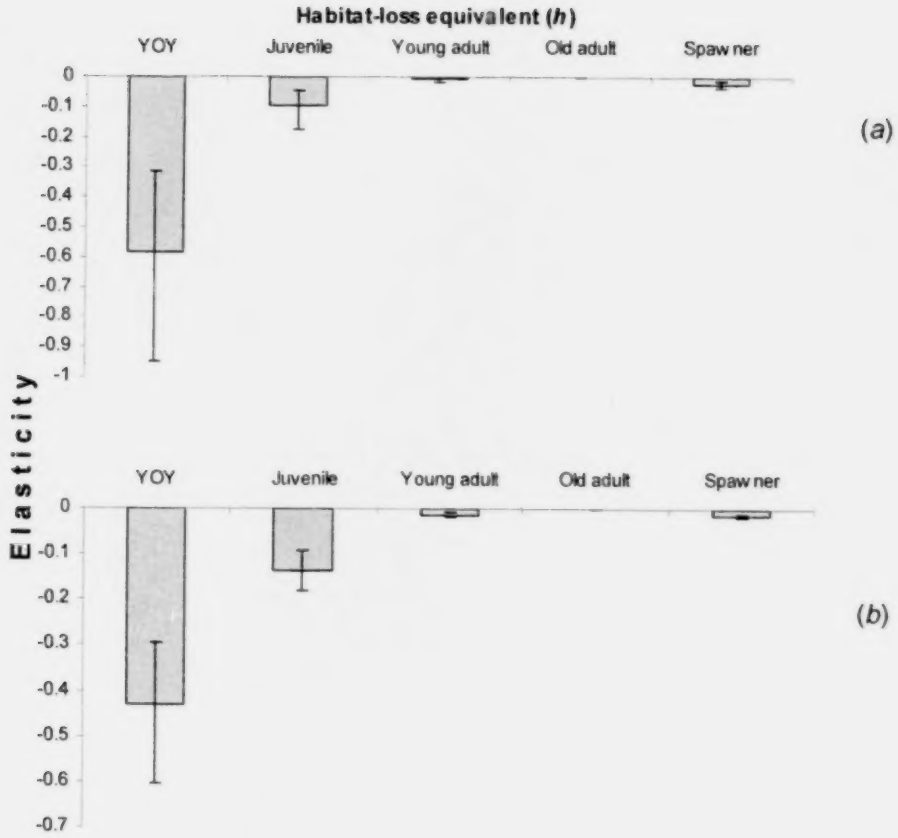


Figure 3. Area equivalent elasticities computed from parametric bootstrap including uncertainty in both, vital rates and habitat-loss equivalents (*a*), and including exclusively uncertainty in habitat-loss equivalents (*b*). Bars indicate 95% confidence intervals.